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THE TAXONOMY OF *MICROCERCULUS* WRENS (TROGLODYTIDAE) IN CENTRAL AMERICA

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The genus *Microcerculus* comprises several species of rather small, stub-tailed, highly terrestrial wrens, denizens of humid tropical and subtropical forest understory. Due to their dense habitat and small size they are seldom observed; were it not for the striking songs of the males (whence their vernacular name of "nightingale" wrens) these birds would often escape notice entirely. It is thus not surprising that there are rather few specimens of these inconspicuous birds in museum collections. This, plus the fact that they have the most complex and variable plumages in the Troglodytidae, have made the nightingale wrens the source of numerous taxonomic problems over the years. In their checkered taxonomic history the nightingale wrens of Central America have been considered to comprise from 1–4 species. For nearly half a century only a single species and subspecies has been recognized in this area (Griscom 1932, Hellmayr 1934, Paynter 1960). However, Slud (1958) called attention to the existence of two very distinct and apparently allopatric song types in Costa Rica, one in the north and the other in the southern part of the country. Although he discoursed at length upon the possible taxonomic implications of divergences in song versus morphology in closely related populations, Slud (1958) never attempted to determine if his song types were in fact morphologically distinct. The present study was undertaken to determine whether two distinct morphological types of *Microcerculus* occur in Costa Rica, and if so whether their distributions coincide with those of the two song types. In the course of this work I have made field observations of the plumage of singing birds, and examined specimens in most major museums. From these studies I conclude that there are two essentially allopatric species of *Microcerculus* wrens in Costa Rica, which differ strikingly in song and

adult plumage, but are often confusingly similar in their variable immature stages.

NOMENCLATURAL HISTORY

In 1861 Salvin described *Microcerculus philomela*, designating as the type an unsexed bird from Vera Paz, Guatemala. Five years later he described *M. luscinia* from two specimens taken at Santa Fé and Santiago, Veraguas, Panamá. In 1888–1889, Ridgway described two additional forms from southern Costa Rica: *daulias* from Talamanca and *orpheus* from Pacuare. The two types were fairly similar in plumage, and evidently Ridgway considered them distinct because he thought that Pacuare was on the Pacific slope, rather than the Atlantic. Realizing his error, he synonymized *orpheus* in 1904 (for original descriptions of these forms see citations in Ridgway 1904); however, he continued to recognize *daulias* (now including *orpheus*) as distinct from *philomela* and *luscinia*. However, soon thereafter Bangs (1909) lumped *daulias* into *luscinia*; he also assigned several recently-taken Underwood skins from northern Costa Rica to *luscinia*, perhaps because of the apparent distributional gap between *philomela* (Guatemala-Chiapas) and the Costa Rican-Panamá birds. Noting the presence of similar plumage types in both populations, he suggested that there might be only one species of *Microcerculus*, *M. philomela*, in Central America, a suggestion enthusiastically accepted by Carriker (1910).

In the next 20 years enough specimens accumulated to show that nightingale wrens were fairly continuously distributed through Middle America, and a detailed analysis was attempted by Griscom (1932). Based on a sample of 38 specimens, Griscom concluded that there was only one species (and one subspecies, *philomela*) in Middle America, as suggested by Bangs (1909). He could see no reliable color characters to separate the Guatemalan *philomela* from specimens of *luscinia* from central Panamá. To accommodate the diversity of plumage types in his sample, he devised a hypothetical plumage sequence of four stages from juvenal to "full adult"—certainly the most complex sequence ever proposed for a wren. He further lumped *philomela* (including *luscinia*) into the South American *M. marginatus*, finding that some specimens from eastern Darién showed some resemblances to certain Colombian birds. Soon thereafter, Hellmayr (1934:282–283 [footnotes]) expressed agreement with Griscom (1932) regarding the Middle American populations. Until very recently, virtually all works on Middle American birds have listed all Middle American *Microcerculus* as *M. m. philomela*. However, following Slud's (1958) description of the two distinct song types in Costa Rica, some authors have adverted the possibility that two species were involved. Blake (1958) mentioned morphological differences (primarily bill color) between a Chiriquí specimen and a series from Chiapas, but concluded that it was an "unlikely possibility" that two species could be distinguished morphologically. Recent popular treatments (Land 1970, Peterson and Chalif 1973) have suggested that *philomela* was specifically distinct from birds from southern Costa Rica south, and Davis (1972) actually treated *philomela* and *luscinia* as separate species on the basis of song (unfortunately, his plate attributes to *philomela* the coloration of *luscinia*, and *luscinia* the coloration of the white-breasted *marginatus* of South America). The illustration in Edwards's (1972) Mexican guide also portrays an adult *luscinia*. Thus, clarification of the morphological picture should benefit field workers as well as systematists. If the two song-types are morphologically distinct, the northern type would be called *philomela*; the name *luscinia* applies to the southern song-type.

METHODS

Although this study consists mainly of a critical analysis of museum specimens, its starting point was provided by direct observations of singing male nightingale wrens. Over the years I was able to observe closely males singing each of the songs described by Slud (1958),

attracting them to within 3–5 m by whistled imitations or playbacks of their songs. The former tactic worked better for the "northern" type of song, but I was unable to imitate the high-pitched southern song well enough to consistently attract the birds. Several of the birds so attracted were also collected and proved to be males; thus, I was able to verify the plumage characteristics of the adult males of the two song types. I should also emphasize that males singing one song-type were never attracted to playbacks or imitations of the other song-type (although my sample size is too limited for statistical analysis). Other field observations that proved helpful included sightings of adults followed by begging fledglings on two occasions at Finca La Selva, where only the northern song-type occurs. Field observations also helped me to fill in the distributional picture presented by Slud (1958).

Starting from my field knowledge of the plumage types of adult males, I began an examination of museum specimens, and quickly found that many females resembled closely their respective adult males and were thus probably adults also: sexual dimorphism was slight at best. The real difficulty came with the large number of birds that were more or less variegated below and thus (by analogy with my observations of known fledglings) immature. As the adult plumage types separated nicely along the same geographical lines as did the song types, I provisionally assumed that the immatures would also, an assumption later substantiated by more detailed plumage examinations and mensural data. For each specimen examined, I measured length of exposed culmen (corrected insofar as possible for distortion of the feathers during preparation), wing chord, and tarsus length. The latter feature proved extremely useful in separating a few doubtful cases. I also include in the mensural samples data from several mist-netted birds, since in no case did their measurements deviate significantly from the means calculated for museum specimens of the same song-type. I concluded that the juvenal plumages are the most heavily variegated in both species, and that a distinctive first basic plumage may also occur, but that both are extremely variable. Because of this variability, young birds of the two forms are sometimes extremely difficult to separate on plumage characters alone; but measurements, confirmed by distribution, permit identification of all specimens seen to date.

SONG TYPES

The northern (*philomela*) song consists of a series of pure clear whistles, given at a rate of ca. 2/sec over a period often exceeding 15–30 sec. The individual notes are ca. 0.4 sec in duration, on an even pitch or slurred, and at frequencies of between 3–6 kHz, with or without evident harmonics. Successive notes are usually on different pitches, such that the song "rises and falls in an arresting manner" (Slud 1958); the overall effect is that of a slightly tone-deaf person whistling a hymn tune. This song is introduced by a short motif of more rapid (ca. 4/sec) slurred notes, each successive one slightly higher in pitch, but all being close to 4 kHz in frequency.

The southern (*luscinia*) song is extremely different, following an opening motif somewhat resembling that of *philomela*. The song proceeds as a series of long-drawn (ca. 0.8 sec), clear piercing whistles that become successively lower in pitch (ca. 7 kHz at start, to ca. 5.5 kHz at the end of the song). The intervals between successive whistles increase from ca. 2 sec at the start to 5–10 sec at the end. The entire song typically lasts 2–4 min. Sonagrams of these two song types became available too late to be included here, but will be published in the near future.

Within the *philomela* song-type, at least, pronounced local song dialects exist. This dialect is among the most "tuneful"; in other dialects the rhythm may be slightly more choppy, the song itself less strikingly melodious. However, the differences between dialects are far less pronounced than the orders-of-magnitude differences in tempo between the two song types: there is never the slightest question as to which song-type any given song pertains. Moreover, in any given locality all the birds seem to sing the same song; at least, I have never heard more than one song per locality. This is in contrast to the situation in many other wrens, in which several to many song types exist in any given local population, and individual birds often include several song types in their repertories (e.g., Kroodsma 1980). On several occasions I have played back or imitated the northern song in the presence of birds singing *luscinia*-type songs, without ever observing any overt response. On the other hand, males singing *philomela*-type songs often respond strongly by answering and approaching, when I imitate a different local *philomela* dialect in their presence (e.g., birds at Carrillo and Volcán Orosí responded vigorously to my imitation of the La Selva dialect).

PLUMAGE TYPES

Northern song-type (M. philomela).—From field observations I had determined that adult males of this form were rich brown above, scalloped with blackish, and dull grey below, heavily and indistinctly scaled with blackish; juvenals were strongly variegated with pale grey and blackish below, rather more heavily marked above than adults. Examination of museum skins leads me to propose the following plumages:

(1) Definitive (Basic): Underparts dull dark grey, heavily scaled with dusky to brownish-black, the scaling most distinct and clear-cut on throat (averages decidedly heavier in males), broadest and most indistinct on chest (which may appear nearly solid blackish). Flanks and abdomen dark brown, more or less scalloped fuscous-black. Upperparts rich dark brown, scalloped with black, most closely on crown. Remiges fuscous broadly edged rich brown; wing coverts fuscous-brown, the greater coverts with subterminal bright brown bar, bordered by dusky; this bar becomes paler towards shaft of feather, where a distinct buffy or whitish dot is usually present, giving appearance of a "wingbar" of pale dots; rectrices blackish brown. Iris dark brown; bill black shading to dark horn color on gonys; tarsi blackish.

(2) Juvenal: More contrastingly marked above and below. Upperparts with dark scaling heavier and often less distinct, or set off by paler subterminal areas near the shafts of the dorsal feathers. Wing pattern like adult but pale spots on greater coverts often whiter and more distinct.

Below dusky blackish, more or less heavily scaled with whitish to pale grey (most heavily marked on throat, which may appear mostly whitish). The pale scaling is in the form of subterminal bars of varying width on otherwise dark feathers (though these often have slate-grey bases). Especially in females, this scaling may be broken up to a greater or lesser extent producing a mottled effect of whitish, grey, and dusky. Abdomen and flanks dark brown, scaled blackish and (faintly) whitish. Bill mostly black, gonys often strongly marked with pale horn color.

(3) Immature (First Basic?): In general resembling definitive basic but scaling of underparts more distinct, especially on lower breast and belly; grey paler, more contrasting with blackish. Dark scaling on breast less heavy, appearing distinctly scaled rather than mostly blackish. Evidently males may sing and breed in this plumage.

Southern song-type (M. luscinia).—From field observations I had concluded that adult males of this song-type were plain brown above with whitish throats and slaty underparts, with at most some brownish or dusky freckling or smudging on the lower breast and belly. Inspection of museum skins allowed me to specify the following plumages:

(1) Definitive (Basic): Throat whitish to (some males) very pale grey, unmarked or the feathers with pale grey bases; breast and belly dull slate, the feathers of the lower breast and belly often tipped or freckled with dull brown. Flanks, abdomen rich dark brown, faintly barred with dusky. Upperparts rich chestnut-brown, mostly immaculate though often lightly scaled dusky on crown. Remiges fuscous-black, broadly margined rich brown; wing coverts fuscous-brown, with a paler, brighter subterminal bar (paler near shaft, but never coalescing into a distinct spot). Iris dark brown; bill black becoming pale to dark horn on gonys; tarsi blackish.

(2) Juvenal: Throat whitish, lightly scaled dusky (especially in males); chest slate-grey, scaled with dark brown and (usually) pale grey, the latter often as a subterminal bar bordered by dusky, base of feather slate; sometimes underparts variegated with all three colors, but with slate-grey predominating on chest; dark bars sometimes broken into spots, giving a "grainy" texture to pattern. Flanks dark rich brown scaled blackish. Upperparts rich dark chestnut-brown scaled with blackish, usually heavily on crown and lightly on back. Wing-coverts patterned as adult but subterminal bar of greater coverts usually strongly paler, even buffy towards shaft, but rarely forming a distinct spot. Mandible mostly horn color, dark towards tip.

(3) Immature (First Basic?): More or less intermediate between juvenal and definitive plumages, more similar to the latter. Throat whitish to pale grey, lightly scaled dusky (more pronounced in males). Chest slate-grey, the feathers with smudgy or mottled brown tips (often more pronounced

in males); lower breast, belly more distinctly scaled with pale grey and dusky, the latter markings often broken and "grainy." Above with scaling on back usually faint to obsolete.

From the foregoing it should be evident that the adults of the two song-types are quite distinct in plumage. In both forms the general tendency is from a more contrastingly marked juvenal plumage to a more uniformly marked or immaculate, less contrasty adult plumage. The great variability in young birds definitely complicates things; in particular, some juvenal southern birds may resemble "first-basic" northern types. Certainly the proposed plumage sequences should be taken as hypothetical at this stage, in the absence of data on skull ossification, returns of banded birds, etc. However, I feel that at least the general direction of change is correct, and the sequences themselves are much more in accord with what is known in the Troglodytidae (see Ridgway 1904) than, for instance, the incredibly complex system of Griscom (1932). The starting point of this Procrustean bed (into which two quite different sequences were forced), was the erroneous assumption that all heavily-scaled birds were immature. Thus, the adult of the northern song-type (dark in color, heavily scaled) was assumed to be the juvenal plumage, the adult of the southern form (pale in color, little or no scaling) the adult, with the various immature forms (dark and light scaling or variegation) constituting several intermediate stages. Griscom (1932) stated that he had representatives of all of his plumage types from throughout the range of the 'species'; having examined all the material available to Griscom plus many more recently taken specimens, I can state categorically that this is not the case. The problems lie in the confusing similarity of the immature plumages of *luscinia* and *philomela*, and in the fact that Griscom's knowledge of distributions of these wrens was understandably incomplete due to the inadequate material available.

MEASUREMENTS

Correlated with differences in plumage between the song-types are differences in measurements (Table 1). In general, the southern song-type (*luscinia*) is the larger bird, sex for sex, being particularly significant in the case of tarsal length (Table 2). Males average larger than females in all dimensions, and this difference is most marked in southern birds. However, because of the possibility of missexed specimens I do not care to push this comparison too far. Nevertheless, tarsal length alone suffices to separate over 80% of all specimens, regardless of sex; those with tarsi below 21 mm are nearly all *philomela*; birds with tarsi over 21.5 mm are nearly all *luscinia*. Using all three measurements at least 90–95% of all specimens can be identified to song-type.

TABLE 1

MEASUREMENTS (MM) OF NIGHTINGALE WRENS (*MICROCERCULUS*) FROM CENTRAL AMERICA

Form	Sex	N	$\bar{x} \pm SD$	Range
A. Exposed Culmen				
philomela	♂	31	16.93 ± 0.54	15.9–18.2
	♀	21	16.86 ± 0.56	16.0–18.1
luscinia	♂	27	18.27 ± 0.77	16.9–20.0
	♀	24	17.89 ± 0.89	15.9–19.4
B. Wing Chord				
philomela	♂	31	55.25 ± 1.24	52.4–58.6
	♀	19	54.41 ± 1.80	51.7–58.3
luscinia	♂	27	57.30 ± 1.93	53.4–62.3
	♀	23	55.32 ± 1.66	52.5–59.2
C. Tarsus				
philomela	♂	31	20.76 ± 0.41	19.9–21.5
	♀	19	20.63 ± 0.52	19.8–21.6
luscinia	♂	27	22.59 ± 0.74	21.3–23.7
	♀	24	21.92 ± 0.64	20.6–23.3
D. Weight (g)				
philomela	♂	7	18.64 ± 1.58	17.4–21.5
	♀	4	17.02 ± 0.47	16.4–17.4
luscinia	♂	5	20.08 ± 1.42	18.2–22.0
	♀	4	17.45 ± 0.48	17.0–18.0

Geographic variation within and between song-types is evaluated in Table 3. In general, significant geographical variation within song-types is lacking, but comparisons between Costa Rican populations of the two yield highly significant differences (all measurements of males, and tarsal length in females). In general, the smaller degree of difference between females of the two song-types reflects the much smaller degree of sexual dimorphism in *philomela*, compared to *luscinia* (cf. Table 2). Indeed, the only geographical comparison among females to yield a significant difference was between the two song-types in Costa Rica with respect to tarsus length. In other measurements female *luscinia* were larger than those of *philomela* in Costa Rica; only in bill length were Costa Rican females notably larger than those of more northern populations of *philomela*. (However, note that such geographical comparisons are hindered by the extremely small Honduras-Nicaragua sample.) In both wing and tarsus, Costa Rican populations of the two song-types are at least as different (and usually more so) as are more allopatric populations. The only within-song-type

TABLE 2

STATISTICAL COMPARISONS (STUDENT'S *t*) BETWEEN MEAN MEASUREMENTS OF DIFFERENT FORMS OF NIGHTINGALE-WREN, AND BETWEEN SEXES OF EACH FORM (ALL SPECIMENS COMBINED)

	Exposed culmen	Wing chord	Tarsus
♂ *luscinia* vs ♂ *philomela*	7.79***	4.76**	13.56***
♀ *luscinia* vs ♀ *philomela*	4.53**	1.69	6.97***
♂ vs ♀ *philomela*	0.78	1.34	0.09
♂ vs ♀ *luscinia*	3.92**	1.49	4.09**

* = $P < 0.05$, ** = $P < 0.01$, *** $P < 0.001$.

comparison to yield a significant difference was tarsus length between the two Panamá samples of male *luscinia*. Males from central and western Panamá tend to have shorter tarsi than do those of either Costa Rica or eastern Panamá (the same is true of females, but the differences are not significant). Only in bill length might there be reason to suspect a clinal change over all populations (with culmen length increasing from north to south), but even here the cline is decidedly 'stepped' between the two song-types in Costa Rica (especially in males). Within Costa Rica I can discern no geographical trends in measurements, but sample sizes from particular areas are too small to permit meaningful statistical analyses. Suffice it to say that the most nearly sympatric populations of the two song-types seem to differ by about as much as do more allopatric populations.

DISTRIBUTION

The known distributions of northern and southern song- and plumage-types in Costa Rica are mapped in Fig. 1. As can be seen, distribution of song-types (based on my field observations and data in Slud [1958]) and plumage types (based on specimens) coincide precisely: there is no question that Slud's (1958) song-types are also morphological entities—two kinds of nightingale wren occur in Costa Rica. Their distributions are essentially allopatric, and with the data now in hand it is possible to specify distributional limits in greater detail than did Slud (1958).

The northern bird, *philomela*, is most abundant in the foothills and adjacent lowlands of the northern half of the Atlantic slope. On the Pacific side it does not occur in lowland Guanacaste, but only in humid-forested ravines along the bases of the Guanacaste volcanos. It is, in my experience, most characteristic of ravines in hilly, forested country; the bird I heard at Tortuguero was not in lowland swamp forest but on the slopes of

a low range of hills ca. 5 km inland from the coast. Its southern limit is the northeastern edge of the Cordillera Central near the town of Guácimo; it ranges north to Chiapas, México. Its upper elevation limit is around 1400 m, but it is not common much above 1000 m in most areas.

The southern bird, *luscinia*, is associated in Costa Rica with the foothills of the Cordillera de Talamanca and the adjacent lowlands. On the Pacific slope of Costa Rica, it ranges north to the hills south and west of the Meseta Central (the south side of the Río Barranca watershed [P. Slud, in litt.]); on the Atlantic slope, to about the northern edge of the watershed of the Río Reventazón. In the Pacific lowlands, its northward distribution is probably limited by the drier conditions north of the mouth of the Golfo de Nicoya; it is also not known from the Meseta Central, which again is somewhat drier than the surrounding hills. Southwards, *luscinia* ranges to eastern Darién, Panamá. In my experience the habitat of *luscinia* is quite similar to that of *philomela*, but it seems perhaps less limited to hilly country, and may be found in old second growth as well as forest (cf. Slud 1964). It occurs from near sea level to about 1200–1400 m on the Atlantic slope, and up to ca. 1700 m locally in the somewhat more seasonal forests on the Pacific slope of the Cordillera de Talamanca.

The ranges of the two forms of *Microcerculus* approach one another closely on both slopes of Costa Rica, but the nature of the contact zone (if any) is difficult to discern at present, perhaps largely due to the severe habitat disturbance in the critical areas. On the Pacific side, the Río Barranca watershed is mostly deforested, and the remnant patches of forest are probably too small and isolated to support viable *Microcerculus* populations. On the Atlantic slope, severe habitat disturbance in the Reventazón drainage dates back over a century. There may be a zone on the northeastern edge of the Cordillera Central where neither species occurs at present. At any rate, I failed to find any *Microcerculus* in remnant forest patches between Siquirres and Guácimo on trips in 1975 and 1979. Prior to habitat disturbance, I suspect that the contact between the two forms was always abrupt, with complete replacement of one form by the other within a short distance, perhaps reflecting competitive exclusion, given their similar ecology and morphology (cf. Diamond 1980). Moreover, I suspect that the sharp dividing line between the two might have been maintained by interspecific territoriality. The similarity of the opening motifs of the songs of the two forms is interesting in this connection. One could hypothesize that it might permit birds of one form to recognize those of the other form as potential territorial rivals, while the rest of the song might help to maintain reproductive isolation, as evidently occurs in meadowlarks (*Sturnella* spp.) (Szijj 1966).

It is interesting that the dividing line between the two forms falls in or

TABLE 3

GEOGRAPHIC VARIATION IN MEASUREMENTS[a] OF *MICROCERCULUS* WRENS OF MIDDLE AMERICA. MEAN MEASUREMENTS FOR DIFFERENT GEOGRAPHICAL AREAS (GUATEMALA-CHIAPAS, HONDURAS-NICARAGUA, COSTA RICA, WESTERN AND CENTRAL PANAMÁ, EASTERN PANAMÁ) ARE COMPARED BY *t*-TESTS.

		Bill		Wing		Tarsus	
Sex, Taxon	Area	Measurement	*t*	Measurement	*t*	Measurement	*t*
Males							
philomela	Guat.-Chis.	16.82 ± 0.46 (12)		55.18 ± 1.30 (12)		20.69 ± 0.38 (12)	
			0.03		0.87		1.66
	Hond.-Nica.	16.80 ± 0.67 (7)		55.65 ± 0.76 (7)		20.98 ± 0.37 (7)	
			0.99		1.20		1.65
	C. Rica	17.12 ± 0.64 (13)		55.10 ± 1.16 (13)		20.68 ± 0.44 (13)	
			3.88**		3.95**		7.59***
luscinia	C. Rica	18.01 ± 0.51 (11)		57.25 ± 1.68 (11)		22.52 ± 0.80 (11)	
			0.76		1.29		1.23
	W. + C. Pan.	18.29 ± 1.04 (7)		56.25 ± 1.64 (7)		22.11 ± 0.66 (7)	
			0.78		1.91		3.19**
	E. Pan.	18.62 ± 0.68 (9)		58.16 ± 2.19 (9)		23.02 ± 0.48 (9)	
Females							
philomela	Guat.-Chis.	16.73 ± 0.30 (11)		54.33 ± 1.68 (11)		20.64 ± 0.41 (11)	
	Hond.-Nica.	16.40 (2)		54.50 ± 1.97 (2)		21.00 ± 0.28 (2)	

TABLE 3
CONTINUED

Sex, Taxon	Area	Bill		Wing		Tarsus	
		Measurement	*t*	Measurement	*t*	Measurement	*t*
	C. Rica	17.07 ± 0.74 (8)	1.73	54.35 ± 1.93 (8)	0.02	20.65 ± 0.69 (8)	1.19
luscinia	C. Rica	17.74 ± 0.86 (6)	1.64	55.88 ± 1.98 (6)	1.52	22.14 ± 0.54 (6)	4.56***
	W. + C. Pan.	17.76 ± 1.04 (10)	0.02	55.75 ± 1.37 (10)	0.16	21.66 ± 0.75 (10)	1.31
	E. Pan.	18.16 ± 0.64 (9)	0.96	54.75 ± 1.56 (10)	1.48	22.03 ± 0.51 (10)	1.29

[a] Measurements given are means, SD, and N.
* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$.

FIG. 1. Distribution of two forms of *Microcerculus* in Costa Rica. Circles = *M. philomela* (northern song-type); triangles = *M. luscinia* (southern song-type); locality records based on song (open figures), specimens (half-solid figures), or both (solid figures). R = Río Reventazón.

near the Reventazón drainage, as this area is evidently a zone of considerable floral and faunal turnover (Stiles 1979). Among the bird species reaching their northern or southern limits in this area are Blue-headed Parrot (*Pionus menstruus*), Sulphur-rumped Tanager (*Heterospingus rubrifrons*), Coppery-headed Emerald (*Elvira cupreiceps*), and *Microcerculus* spp. (cf. Slud 1958, 1964). In plants, several different taxa of *Heliconia* meet and hybridize in this area (Stiles 1979), and considerable turnover occurs in several other groups as well (J. Gómez Laurito, pers. comm.).

Considerable species turnover also occurs here in butterflies (P. J. De Vries, pers. comm.).

The geological and historical reasons for this degree of turnover in this area are obscure. One possibility is that the different forms have spread from different Pleistocene wet-forest refugia, although the exact locations for these are still somewhat conjectural (cf. Muller 1973, Haffer 1974). The Cordillera Central and the Cordillera de Talamanca are roughly the same age (early Pleistocene) in their present forms (Lloyd 1963), but even small differences in the timing of their respective upliftings might have had major effects on their respective biotas. In any case, historical factors must be implicated in trying to explain the degree to which 'suture zones' in so many animal and plant groups coincide in an area of such essentially uniform climate and vegetation as the Caribbean lowlands of Costa Rica. The fact that the Río Reventazón is the major river draining the area between the two cordilleras suggests that the latter must have had a major effect, perhaps in producing the weather patterns responsible for Pleistocene refugia.

CONCLUSIONS

Based upon song type, morphology, and distribution, I have no hesitation in calling the two *Microcerculus* wrens of Costa Rica distinct species. I have never seen an adult specimen that I could confidently call a hybrid, nor have I ever heard an intermediate song. At present I know of no area where the two forms are sympatric, though an exhaustive survey of the area around the Reventazón drainage might be enlightening in this respect. The similarity in immature plumages and the difficulty of identifying young birds by plumage alone is neither surprising nor distressing: it is the adult plumages and songs that will function as isolating mechanisms. The northern bird should be called *Microcerculus philomela* Salvin. Given the irregular or clinal nature of the variation within this form, recognition of subspecies is unwarranted. The exact status of *luscinia* Salvin is uncertain, for it may be conspecific with one or more members of the South American *M. marginatus* complex, which, as currently constituted, includes several forms rather different in appearance. Closest geographically to *luscinia* are the transandean forms *taeniatus* and *squamulatus*, with scaly-grey breasts in all plumages; true *marginatus* occurs east of the Andes and has a plain white breast. Various observers report that birds of these forms from a wide area in northern South America (from Venezuela to Perú) give *luscinia*-like songs (fide E. Eisenmann, B. Coffey, J. Fitzpatrick, R. Ridgely, P. Schwartz). On the other hand, in Perú there is great variability in song-type, with the song from southern Perú sounding

quite different from either *philomela* or *luscinia* (fide J. Fitzpatrick). All Peruvian birds are currently classified as a single subspecies, *marginatus*; indeed, the situation seems suspiciously reminiscent of that in Middle America, and a great deal of field and museum work will be required to resolve it. For the present, I think it most convenient to emphasize the morphological picture in Central America by considering *luscinia* a species (or semispecies), pending detailed study of South American birds.

With respect to English vernacular names, it is worth noting that "nightingale-wren" was originally applied by Salvin only to *philomela* (which he had doubtless heard in Guatemala), and was later extended to allied forms without benefit of voice data. The song of *luscinia* and its allies in no way resembles that of a nightingale (for that matter, neither does that of *philomela*, except in its possession of strikingly musical quality). Taking voice into account (since the birds are far more often heard than seen), I would recommend that the group name "nightingale-wren" be restricted to *philomela* (which would be called simply Nightingale-Wren). I agree with a suggestion by E. Eisenmann that "whistler-wren" would be an appropriate group name for those birds singing *luscinia*-like songs. If *luscinia* is considered a species or semispecies in its own right, it could be called Northern Whistler-Wren. Should the entire complex be considered as a single species, the unmodified name Whistler-Wren would of course suffice for all.

SUMMARY

Evidence from morphology and distribution is combined with data on song to demonstrate the existence of two species of *Microcerculus* wrens in Central America: *M. philomela* Salvin (Nightingale-Wren), ranging from Chiapas, México, to central Costa Rica; and *M. luscinia* Salvin (Northern Whistler-Wren), which ranges from central Costa Rica to eastern Darién, Panamá. The importance of the Reventazón region of the Caribbean slope of Costa Rica as a zone of faunal and floral turnover is indicated. Perhaps because of habitat disturbance and/or ecological incompatibility, there is no known area of sympatry of the two forms at the present time.

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Specimens were examined from the following museums (numbers in parentheses are specimens of *philomela* and *luscinia*, respectively): American Museum of Natural History (8, 14); British Museum (Natural History) (8, 1); Field Museum of Natural History (7, 2); Loui-

siana State University Museum of Natural History (5, 2); Museum of Comparative Zoology (8, 8); Museo Nacional de Costa Rica (0, 2); Museo de Zoología, Universidad de Costa Rica (3, 1); University of Michigan Museum of Zoology (1, 1); U.S. National Museum (1, 17); University of California, Los Angeles (2, 1); Western Foundation of Vertebrate Zoology (4, 1). In addition, data from four *philomela* and three *luscinia*, mist-netted, measured, and released, are included.

LITERATURE CITED

Bangs, O. 1909. Notes on some rare or not well-known Costa Rican birds. Proc. Biol. Soc. Washington 22:29–38.

Blake, E. R. 1958. The birds of the Volcan de Chiriqui, Panama. Fieldiana: Zool. 36:499–577.

Carriker, M. A., Jr. 1910. A list of the birds of Costa Rica, including Cocos Island. Ann. Carnegie Mus. Nat. Hist. 6:314–615.

Davis, L. I. 1972. A field guide to the birds of Mexico and Central America. Univ. Texas Press, Austin, Texas.

Diamond, J. 1980. Why are many tropical bird species patchily distributed in available habitat? Pp. 968–973 *in* Proc. XVII Int. Ornithol. Congr., Berlin, West Germany.

Edwards, E. P. 1972. A field guide to the birds of Mexico. E. P. Edwards, Sweet Briar, Virginia.

Griscom, L. 1932. The ornithology of the Caribbean coast of extreme eastern Panama. Bull. Mus. Comp. Zool. 72:302–372.

Hellmayr, C. E. 1934. Catalogue of birds of the Americas, Pt. 9. Field Mus. Nat. Hist. Publ. 347, Zool. Ser. No. 13.

Haffer, J. 1974. Avian speciation in tropical South America. Publ. Nutt. Ornithol. Club, No. 14.

Kroodsma, D. E. 1980. Winter Wren singing behavior: a pinnacle of song complexity. Condor 82:357–365.

Land, H. C. 1970. The birds of Guatemala. Livingston Publ. Co., Narberth, Pennsylvania.

Lloyd, J. J. 1963. Tectonic history of the South Central American orogen. Amer. Assoc. Petro. Geol., Memoir 2:88–100.

Muller, P. 1973. Dispersal centers of terrestrial vertebrates in the Neotropical realm. Biogeographica 2. W. Junk, The Hague, The Netherlands.

Paynter, R. A. 1960. Pp. 435–436 *in* Check-list of birds of the world, Vol. 9 (E. Mayr and J. C. Greenway, Jr., eds.). Harvard Univ. Press, Cambridge, Massachusetts.

Peterson, R. T. and E. L. Chalif. 1973. A field guide to Mexican birds. Houghton-Mifflin, Boston, Massachusetts.

Ridgway, R. 1904. The birds of North and Middle America, Pt. 3. U.S. Natl. Mus. Bull., Vol. 50.

Slud, P. 1958. Observations on the Nightingale Wren in Costa Rica. Condor 60:243–251.

———. 1964. The birds of Costa Rica: distribution and ecology. Bull. Am. Mus. Nat. Hist., Vol. 128.

Stiles, F. G. 1979. Notes on the natural history of *Heliconia* (Musaceae) in Costa Rica. Brenesia 15, Suppl. 151–180.

Szijj, L. 1966. Hybridization and the nature of the isolating mechanism in sympatric populations of meadowlarks (*Sturnella*) in Ontario. Z. Tierpsychol. 23:677–690.

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